

## NUTRIENT CYCLES IN OAKWOOD ECOSYSTEMS IN NW ENGLAND

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### Introduction

Studies of the processes and functioning of ecosystems form one way in which we can increase our understanding of the natural environment, and hence the impact of man's activities on it. Such a whole ecosystem approach may include studies of production or the flow of energy through the system, but both of these processes are dependent on the availability of nutrients which, in most cases, is dependent in turn on their being recycled. An important approach, therefore, is to determine and evaluate the cycle of major plant nutrients, together with the losses and gains for the entire ecosystem. Those losses and gains which occur naturally, ie nutrients leached from the ecosystem through the soil into the rivers on the one hand, or gained in rain, dust etc on the other, are also part of a cycle, although a very much larger one in which materials circulate between the land, rivers, oceans and atmosphere.

The cycle (within ecosystems) consists of the uptake of nutrients mainly in simple inorganic form from the soil or atmosphere; the, at least partial, incorporation of these nutrients into more complex organic materials within the plants, some of which are retained as current production of roots, stems, branches and shoots; and the return of the remainder to the soil surface, by the leaching action of rainfall, as litter fall, or through death of the plants. On becoming re-mineralised, the nutrients in this dead organic material are again taken up by the vegetation. Additionally, there is normally a subsidiary cycle via secondary producers, ie plant-eating animals, either vertebrate or invertebrate which in turn provide food for predators. Unassimilated materials (faeces) and, subsequently, the dead bodies of the animals also join the organic debris. Nutrient-cycling is the major expression, within the ecosystem, of the interaction between plants and soils, and is also of significance in the formation of the soil itself. Arguably, therefore, it can be considered the most important single basis for analysing an ecosystem, although a combination of approaches is necessary for the fullest understanding.

Studies on this theme have been carried out at Merlewood since it was established as the Nature Conservancy's first research station 20 years ago. Oakwood, using the term in a fairly broad sense, was selected as the ecosystem on which to concentrate such studies,

being the typical local native woodland, and the presumed climatic climax. It thus provided a good base-line against which more disturbed or artificial ecosystems could later be compared. Because Silurian slates and Carboniferous limestone both occur within the neighbourhood of Merlewood it has been possible to study the two contrasting oakwood systems which these geological formations support. The two types are exemplified by the two main research areas: Bogle Crag on slate, and the Carboniferous limestone site of Meathop Wood, which is a main woodland site within the International Biological Programme. Earlier studies had been made at Roudsea Wood National Nature Reserve where, interestingly, the slate and limestone occur side by side in the same wood. The present paper attempts to present a very general picture of the cycle of nutrients in oakwoods based on the complementary studies made at these two main sites, and will briefly draw comparisons between them and with other woodland ecosystems. In order to facilitate such comparisons, and for the sake of simplicity, the above-ground data only are considered. Similarly, only the net annual changes will be examined, although of course, there is much seasonal variation in nutrient flow and some cycles can occur over a shorter time than one year. A detailed account of the Meathop work, including studies of the below ground components, is currently being prepared<sup>1</sup>.

#### Site descriptions

##### 1. *Bogle Crag*

Bogle Crag Wood (9.3 ha, 23 acres) part of the Forestry Commission's Grizedale Forest in NW Lancashire, is 90–140m (290–460ft) above sea level, with a western aspect. The soil is a well-drained, acid brown earth, with a mean pH of 4.5 and a moderate humus, overlying Silurian slates and mud-stones of the Bannisdale series. Mean annual rainfall is 171cm (67.5in). Apart from small flushed areas, the woodland is dominated by a single-storey high forest (but derived from former coppice) of Sessile oak (*Quercus petraea*) with a few scattered birch (*Betula* spp). At the time of the studies (1961–1965), the trees were in the main about 80 years old (although varying from 40–120 years) with 158 trees/ha. The canopy was 90–95% closed. The ground flora mainly consists of Wavy hair-grass (*Deschampsia flexuosa*) and bracken (*Pteridium aquilinum*) [This woodland corresponds with the A1 to B1 type described by Steele (p. 131).—Ed.]

##### 2. *Meathop Wood*

Meathop Wood (c. 45m, 150ft, above sea level) is a research area, which is part of a larger area (40ha, 100 acres) of woodland on the outcrop of Carboniferous limestone, with terraces and small scarps, known as Meathop Fell. On the south side, the wood is within about 300m of the estuary of the R. Kent (Morecambe Bay). The terraces are covered with a variable, but mainly shallow, layer of glacial drift, giving rise to a brown earth with mull humus and a pH (4.1–7.5) which varies markedly, mainly with the depth of soil

and hence the influence of the underlying limestone. Mean annual rainfall is 124cm (48.5in).

Meathop is a mixed deciduous woodland; oak, ash and birch of varying age, dominate the upper canopy, with smaller proportions of sycamore, Wych elm and other tree species. A variable, but usually well-developed, under-storey is present, consisting of hazel with some hawthorn, ash and calcicole shrub species. The ground layer is species rich, but is dominated by *Mercurialis perennis*, *Rubus vestitus* and *Brachypodium sylvaticum* together with *Endymion non-scriptus*, *Anemone nemorosa*, *Oxalis acetosella* and many other herb species. Studies started in 1965, and are still continuing. [This woodland type falls into the B2 to C1 categories of Steele (p. 132).—Ed.]

### The components of the cycle

Although information on transfers from soil to roots, and subsequently to the various parts of the trees, is not available in detail, the remaining components of the oakwood cycle may now be examined in more detail. Full descriptions of the methods used at the two research sites are given elsewhere (Carlisle et al.<sup>2 3 4</sup> for Bogle Crag; Satchell<sup>1</sup> for Meathop) and will not be repeated here. All sampling, however, was related to units of known area such that by combining weights (or volumes in the case of water) with the concentrations of nutrients given by chemical analysis, the absolute quantities of nutrients per unit area of woodland (kg/ha) could be determined for the various components.

#### 1. Nutrients retained in tree increment

Information on the nutrients retained in the net increment of the trees is dependent on first establishing the dry weight increment of the stand. This is conveniently done by determining increases, over a period of say 5 years, in total stand biomass the latter being obtained from the relationship (derived from felling sample trees) between the girths of all trees in a given area and their dry weights. Chemical analysis of the various biomass components enable the total nutrients present in the stand to be calculated, together with the additional quantities retained annually. Data are presented in tables 5 and 6. Shrub data for Meathop are included with the trees, as will be the case throughout this paper; no shrubs were present in the sampled areas of Bogle Crag.

#### 2. Litter fall

The most obvious route of return between trees and the forest floor is by the autumn leaf fall. There are, however, many other types of litter which provide additional transfer paths, some very appreciable. In the spring, the bud scales and catkins fall, together with a number of young leaves, especially in windy weather. Later the peduncles with or without acorns, add to the litter, and, throughout the year, dead branches, twigs, fragments of bark and other materials contribute considerable quantities of litter. All these litter fractions can be sampled using suitable collecting vessels;

TABLE 1

The quantities of nutrient elements in different types of oakwood litter falling annually: Bogle Crag and Meathop  
(Kilograms/hectare)

Part of tree	Dry weight		N		K		Ca		Mg		P	
	Bogle Crag	Meathop	Bogle Crag	Meathop	Bogle Crag	Meathop	Bogle Crag	Meathop	Bogle Crag	Meathop	Bogle Crag	Meathop
Leaves	2126	3251	21.1 (51.3%)	39.5 (54.4%)	6.3 (59.9%)	17.2 (68.2%)	16.8 (70.4%)	57.0 (74.2%)	2.7 (70.8%)	8.6 (71.1%)	0.92 (42.0%)	2.26 (52.1%)
Twigs and branches	1163	1776	7.7 (18.8%)	12.8 (17.6%)	1.6 (15.0%)	3.2 (12.7%)	4.2 (17.5%)	14.2 (18.5%)	0.5 (13.7%)	2.1 (17.35%)	0.39 (17.8%)	0.72 (16.6%)
Miscellaneous debris	568	709	12.3 (29.9%)	20.3 (28.0%)	2.6 (25.0%)	4.8 (19.0%)	2.9 (12.1%)	5.6 (7.3%)	0.6 (15.5%)	1.4 (11.6%)	0.88 (40.2%)	1.36 (31.3%)
Total	3857	5736	41.1	72.6	10.5	25.2	23.8	76.8	3.9	12.1	2.19	4.34

Percentages of the total for each element per site given in parentheses.

Note: Some of the Meathop data are provisional and subject to revision in Satchell<sup>1</sup>

different types of litter were collected in containers appropriate to the size of the litter materials. Samples must be removed frequently from the collecting vessels to avoid changes in nutrient content through leaching, respiration or decomposition. Dry weights of these various types of litter, together with chemical analyses, for each month throughout the year, permit their role in the nutrient cycle to be assessed. Results are given in table 1 which demonstrate the significance of the non-leaf litter, and in particular, the role of the miscellaneous debris in the phosphorus cycle. The monthly data also enable the importance in the cycle of the litter falling in spring and summer to be seen. Bogle Crag data presented in table 2 suggest that more P, and almost as much N and K, are returned to the forest floor in the litter of spring and summer as fall in the period of main autumn leaf fall. Only small amounts return in winter litter.

TABLE 2  
Seasonal pattern of litter fall nutrients: Bogle Crag  
(Kilograms/hectare)

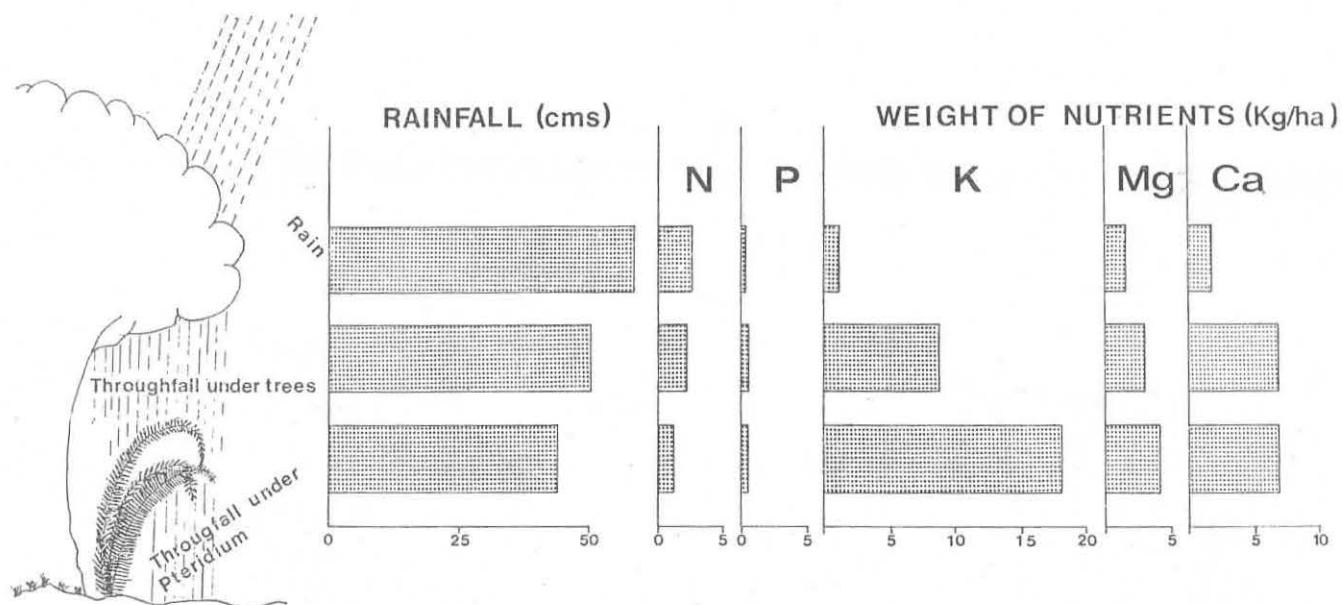
Season	N	K	Ca	Mg	P
Spring and Summer (April-September)	18.4 (45%)	4.5 (43%)	6.5 (27%)	1.21 (31%)	1.19 (55%)
Autumn (October-December)	21.6 (53%)	5.9 (56%)	17.1 (72%)	2.63 (68%)	0.94 (43%)
Winter (January-March)	1.0 (2%)	0.1 (1%)	0.2 (1%)	0.03 (1%)	0.04 (2%)
Total .. ..	41.0	10.5	23.8	3.87	2.17

*Percentages of total for each element in parentheses.*

### 3. *Leachates*

A less conspicuous pathway for nutrient return is that resulting from the action of rainfall. Chemical analysis of rainwater shows that it has a small, but ecologically significant, content of plant nutrients (table 3). However, a comparison made of rainfall collected above the woodland canopy or outside the wood with that sampled beneath the canopy, shows that in dripping through the tree leaves, twigs and branches (throughfall), rainwater is considerably enriched in the bases K, Ca and Mg. Conversely, inorganic N is regularly removed from the rainwater, and in some months total N (ie inorganic+organic), together with P, are also reduced, probably by micro-organisms in the canopy, or possibly through foliar absorption (fig 1). The rain which runs down the main branches and the trunks (stem flow) is even richer in base elements. A good deal of this enrichment, but not all, is due to the leaching of nutrients out of the canopy, mainly from the foliage, but possibly in part from micro-organisms present on the foliage, but derived directly or indirectly from the trees' tissues and therefore part of the cycle.

FIGURE 1



Quantities of nutrients (kg/ha) in rainwater above and beneath the canopy at Bogle Crag Wood, NW England, for the period July–October inclusive.

A proportion of the enrichment, however, has a quite different source, being derived by the washing from the tree crowns of particulate matter, aerosols and dust, which have been 'filtered' from the atmosphere by impaction on the canopy, (ie matter which is additional to the similar material removed from the atmosphere in the rain, and which is largely responsible for the nutrient content in ordinary rainfall). This widely reported phenomenon has been discussed by White and Turner<sup>5</sup>. The practical value of trees for filtering particulate matter from the air, including radioactive particles and other pollutants has been studied in Germany<sup>6 7</sup>. In the present context, we clearly need to be able to distinguish between throughfall enrichment due to nutrient circulation and that resulting from impaction, which represents additional income to the ecosystem. Within the Meathop Wood Research programme, White has developed a method for obtaining a weekly sample through the year of the particles trapped on filter-paper discs, simulating leaves, exposed to air movements but shielded from rain. The equipment used, together with other meteorological instruments, was supported on a tower at mid-canopy level. A factor was obtained to convert quantities recovered from simulated leaves to estimates of the amount caught on the actual leaves present in a given area of woodland canopy<sup>5</sup>. The results given in table 3 suggest that nutrient income from the impactation of aerosols on the woodland canopy is comparable with that in the rainfall.

TABLE 3  
Atmospheric income of nutrient elements: Meathop  
(Kilograms/hectare)

	N	K	Ca	Mg	P
Rainfall ..	5.9 (+N fixation)	3.2	6.9	5.4	0.23
Aerosols ..	—	3.4	1.8	8.4	0.12
Total ..	5.9+	6.6	8.7	13.8	0.35

#### 4. *Ground flora*

The role of ground flora has been assessed by periodic harvesting throughout the year. It parallels in most respects the role of the tree; nutrients are taken up and returned annually by adding to the litter, although some would also be retained if a steady state had not been reached (ie if annual biomass were increasing). In both research sites it has been assumed that the latter is not the case and that all uptake in the herb layer is recycled. The quantities involved are given in table 4. Materials are also leached from ground flora by the rain. In studies at Bogle Crag, the enriched throughfall from the tree canopy was shown to be further enriched after passing over bracken fronds. These data were obtained by allowing newly emerged fronds in the spring to grow through slits in the polythene floor of a

number of frames. Subsequently, the rachides were sealed into place with an inert sealing compound. The natural slope of the ground facilitated collection of waters from the lowermost corner of each frame. The results are demonstrated in table 4 and fig 1, and show the appreciably increased cycling of magnesium and potassium which results, but that little extra calcium was cycled in this way.

TABLE 4

Nutrient elements cycled by leaching from bracken and in its litter: Bogle Crag  
(Kilograms/hectare)

	N	K	Ca	Mg	P
Bracken litter ..	12.9	6.9	4.0	1.3	0.89
Leached from bracken ..	-0.3	9.4	0.1	1.0	0.09

#### 5. *Herbivores*

The litterfall and leaching pathways by which nutrients are returned to the forest floor, appear to be essential or 'obligatory' parts of the cycle. A 'non-obligatory' route is provided by herbivores and any associated carnivore food-webs. Despite the great diversity of different animals, especially invertebrates, associated with oak—or perhaps because of it, in that their diversity inhibits the build-up of over-large numbers—the quantitative role of animals in the nutrient cycle is usually small and hence has been omitted from the main nutrient cycle tables and diagram. At Meathop, the numbers of defoliators appear to have been consistently very low. On slate sites in the district however, populations of *Tortrix viridana* build up from time to time, possibly related to the markedly reduced species diversity amongst trees and other plants on such sites compared with the woodlands on limestone. At Bogle Crag, there was a moderately severe defoliation by the larvae of *Tortrix* in 1961 but only low numbers in the other years during the period under study (1961–1965). The role of such defoliation in the nutrient cycle was studied by sampling the frass falling to the ground, and by obtaining a conversion factor in order to relate the weight of frass to the weight of foliage consumed. Numbers of leaves eaten were also sampled. The effects of such defoliations are discussed later.

#### 6. *Litter decomposition*

Nutrients falling to the forest floor in the litter cannot, for the most part, re-enter the uptake cycle again until they are made available (mineralised) by the activities of the decomposer organisms. The decomposition stage, therefore, is a critical one without which litter would accumulate indefinitely, nutrients would remain organically 'locked up' and unavailable, and the soil conditions become radically altered—as happens when excessive raw humus formation occurs or, more extremely, with peat formation. On the other hand, the drawn out processes of mineralisation provide a regulatory mechanism whereby nutrients are provided continually



and steadily for re-use, and, in the main, prevented from being washed out of the ecosystem. It has been shown that woodlands can be very efficient at retaining their nutrients, the latter being rapidly lost into streams and rivers if the forest is cleared<sup>8</sup>.

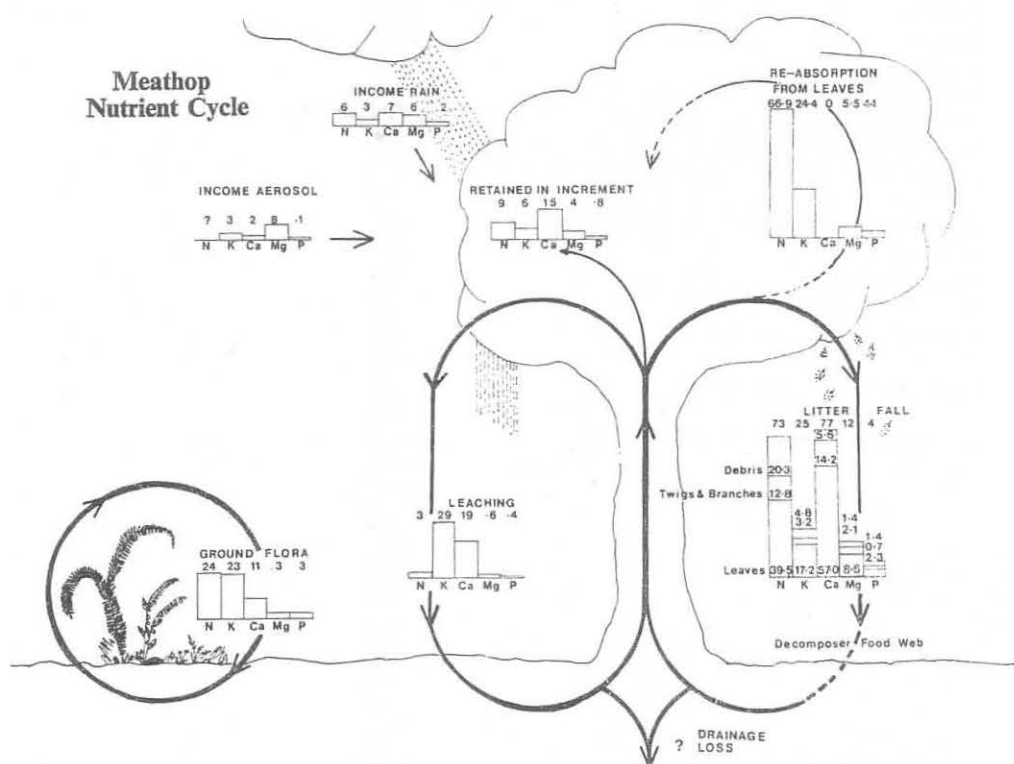
The bulk (80–90%) of the decomposition is carried out by micro-organisms<sup>9</sup>, ie bacteria, fungi and actinomycetes. However, their normal role appears to be at least partly dependent on the catalytic effects of soil animals, whose feeding activities aid decomposition in a number of ways<sup>10</sup>. The resulting food-web is of great complexity and involves very many species, but the more important organisms in base-rich oakwoods are earthworms (*Oligochaeta*), springtails (*Collembola*), millipedes (*Diplopoda*) and nematode worms. In more acid sites, such as Bogle Crag, earthworm activity is markedly reduced, but springtails and mites assume greater importance; the importance of fungi relative to bacteria also increases. Because of the essential role of decomposers in ecosystem functioning and because of the complexity of the process, this aspect of ecosystems in general has probably received greater attention than any other. Details of such work are outside the scope of this paper but, for Bogle Crag, studies limited mainly to the role of fungi, have been published by Hering<sup>11, 12</sup>; the fuller information for Meathop is given in Satchell<sup>1</sup>.

In contrast to the nutrients returning in the litter fall pathway, where availability for re-use is delayed to a greater or lesser extent, those falling to the forest floor by leaching are immediately reusable either by the trees and other plants themselves or by the micro-organisms in the litter. These leached nutrients may thus serve these organisms in their vital role of litter decomposition by providing a rapidly utilisable nutrient source. Similarly, the soluble carbohydrates, mainly sugars resulting from the honey-dew of aphids which are also washed from the canopy in the summer<sup>13 14</sup>, may furnish them with a readily assimilable energy source.

#### Nutrient uptake and cycling

Having presented information on the various parts of the cycle, the overall picture obtained (table 5 and fig 2) can now be considered and discussed. Net annual uptake consists of the sum of materials retained, together with those returned in the cycle. Gross uptake will be greater if shorter term cycles or movements within the tree take place during the year, as indeed appears to be the case. For example, during the growing season, there are variations in the absolute nutrient content of the foliage. At Bogle Crag, phosphorus content reached a maximum in May-June, followed by peaks for nitrogen and potassium and magnesium in late June, whereas calcium content behaved quite differently and continued to rise until the autumn. Apart from this last element, the absolute quantities of these nutrients have considerably lessened by the time the leaves fall, partly through the leaching losses already referred to, but also through a process of nutrient conservation whereby

FIGURE 2



Quantities involved (kg/ha/year) in the above-ground nutrient cycle at Meathop Wood, NW England.

materials are translocated back into the tree before leaf fall and do not therefore enter the external cycle. This 'internal cycle' is especially marked in the case of phosphorus and nitrogen. The maximum foliar levels and the amounts which are re-absorbed in this way (allowances having been made for leaching) for Meathop are shown in the table and figure. Although the full data are not available for Bogle Crag, there are strong indications that this process is even more marked for phosphorus and nitrogen but less so for potassium and magnesium<sup>5</sup>. The quantities of nitrogen re-absorbed are so large (at Bogle Crag equivalent to almost half the total nitrogen in the above-ground biomass) as to lead to the speculation that some may be translocated out of the tree entirely, via root exudates.

Large amounts of nutrients are required by the tree leaves for their development anew each spring and for their subsequent activity as the ecosystem's principal energy-fixing zone. The foliar peaks for nitrogen, potassium and magnesium coincide with the period in

TABLE 5  
Net annual quantities of nutrients taken up and recycled: Bogle Crag and Meathop  
(Kilograms/hectare)

	Dry weight		N		K		Ca		Mg		P	
	Bogle Crag	Meathop	Bogle Crag	Meathop	Bogle Crag	Meathop	Bogle Crag	Meathop	Bogle Crag	Meathop	Bogle Crag	Meathop
(1) Retained in above ground increment (estimated from stem data at Bogle Crag) As % of total uptake (7)	1326	3964	2.5	9.2	1.9	5.9	1.5	14.6	0.25	3.8	0.29	0.78
			(5.6%)	(10.8%)	(6.3%)	(9.9%)	(3.8%)	(13.2%)	(2.4%)	(23.0%)	(9.6%)	(14.1%)
(2) Cycled in all types of litter	3857	5736	41.1	72.6	10.5	25.2	23.8	76.8	3.9	12.1	2.19	4.34
(3) Cycled in leachates (no allowance for aerosols at Bogle Crag)			0.9	3.3	17.5	28.5	14.2	19.3	6.2	0.6	0.55	0.40
(4) Cycled in ground flora (no allowance for ground flora leaching at Meathop)	1470	1031	12.6	24.3	16.3	23.0	4.1	11.0	2.3	3.3	0.98	2.66
(5) Maximum leaf content			105.4	97.2	24.2	46.9	26.3	47.5	6.6	10.3	6.6	6.45
(6) Resorption from leaves				66.9		24.4		0		5.5		4.09
(7) Total net tree uptake (1)+(2)+(3)			44.5	85.1	29.9	59.6	39.5	110.7	10.35	16.5	3.03	5.52

Note: Some of the Meathop data are provisional and subject to revision in Satchell<sup>1</sup>

mid-summer when the amount of daylight available for photosynthesis is also at a maximum. At this time, the leaves contain high proportions of the total nutrients present in the vegetation; at Bogle Crag, 61% of the nitrogen, 52% of the phosphorus and somewhat smaller proportions of the other elements<sup>15</sup>; because of the greater total biomass relative to foliage at Meathop, percentages for this site (derivable from tables 5 and 6) are lower. At both sites, these peak requirements of the leaves are greater than the net quantities cycling in the case of nitrogen and phosphorus—again emphasising the internal cycle—and are a high proportion of the cycled potassium and magnesium. Conversely, considerably more calcium is cycled than is apparently required by the leaves.

Annual retention by the trees in their new growth is also shown. Most of these retained materials are incorporated into the sapwood and bark. The latter is rich in most elements, especially calcium, 75% of the total calcium present in Bogle Crag in the above ground vegetation being in the bark. Although the new extension shoots (1 year twigs) are also rich in nutrients, their dry weight biomass, and hence absolute nutrient content is small.

#### 1. *Nitrogen*

Nitrogen is taken up by the trees as a whole in greater amounts than any other element at Bogle Crag, and is exceeded only by calcium on the limestone site of Meathop. At both sites, nutrient uptake by the leaves was greatest for nitrogen. Very little of this leaf N is leached out and only about a third of it falls in the leaf litter, the larger portion returning to the tree; an amount approaching that in the leaf fall, however, also falls in the non-leaf litter. This large internal cycling of nitrogen has already been referred to; it is also reported to be a marked feature of some grassland systems<sup>16</sup>. In the ground flora, nitrogen, is again taken up more than other elements, but is only about a quarter of the maximum tree uptake. The reduction of the nitrogen content of the throughfall in some months compared with incident rainfall has already been noted. There was further diminution of nitrogen in the bracken leachate at Bogle Crag.

At the same time, large quantities of nitrogen from the air are added to the system by nitrogen-fixing organisms. This probably includes appreciable amounts on the leaves, with even more fixed in the soil. Thus, at Meathop, preliminary results suggest that 109kg/ha is fixed annually, compared with only 12kg/ha lost in drainage. Insofar as nitrogen is not a normal constituent of soil parent material, ecosystems in general must be dependent on acquiring nitrogen through income by fixation or otherwise; the accumulation of nitrogen appears to be especially marked however in woodlands, and Duvigneaud and Denaeyer-De Smet<sup>17</sup> quote high figures for this phenomenon in a wide range of forest types. Nitrogen does not appear to be a limiting factor, even at Bogle Crag, judging from studies of the nutritional requirements of oak on these soils<sup>15 18</sup>.

## 2. *Potassium*

Potassium shows a marked contrast with nitrogen in its behaviour in the cycle. This very mobile element is easily washed from the tree by rain, and the leaching pathway accounts for more than half the potassium cycle in the trees. Of the smaller remaining portion falling as litter, about two-thirds is in the leaf fall. The significance of the ground flora in the potassium cycle is greater than for any other element. At Meathop, the ground flora provided more of this element in its litter than fell in the tree leaf fall, and indeed almost as much as fell in all types of the tree litter (cf tables 1 and 5). The studies in bracken at Bogle Crag showed that, for this species at least, as with the trees, potassium was leached out of it during the summer in larger quantities than fell in its litter.

## 3. *Calcium*

Although leaf uptake is dominated by nitrogen, at Meathop uptake by the trees as a whole is greater for calcium than for any other element. Even at the base-poor Bogle Crag site, the total vegetation biomass contains more calcium than any other element, three quarters of which is in the bark of the trees. Unlike other elements, calcium also continues to accumulate in the foliage, well past the period of maximum leaf weight and activity, and indeed until leaf fall; leaf fall is the major pathway of return for calcium. Calcium differs from other elements also in the quantities lost in the drainage water. Several studies quoted by Duvigneaud and Denaeyer-De Smet<sup>17</sup> show that drainage losses of nutrients from forest ecosystems are all very small except for calcium; data from Meathop support this finding. The very large accumulation of calcium in the bark and in the senescent leaves and the removal of calcium in the drainage water, suggest that calcium is present in the system and is taken up in amounts greater than those required for metabolic activity. It is tempting to speculate that, far from needing to conserve this element, strategems are employed, even on an apparently base-poor site such as Bogle Crag, to remove calcium from the cycle. Apparent luxury uptake is even more marked at Meathop.

## 4. *Phosphorus*

Of the macro-nutrients under discussion, phosphorus is present in much the smallest amounts, both in total, and circulating in the ecosystem. In other respects, it largely parallels nitrogen, with an efficiently conservative cycle. Phosphorus is held closely in the metabolising leaves; little is leached out and in some months none at all. The young, rapidly expanding leaves require relatively large amounts of phosphorus in the spring but, as with nitrogen, a marked internal cycle operates in which two thirds of this peak quantity is re-absorbed before leaf fall. The leaf litter contains only half the total litter fall phosphorus, much of the remainder being in the miscellaneous debris fraction which includes the phosphorus-rich catkins and budscales falling in spring. Although very little is washed out of the foliage when living, there is evidence that phosphorus is lost relatively quickly after the leaves have fallen. The phosphorus

content of Bogle Crag litter was reduced by 60% in just six weeks from leaf fall, a proportion only exceeded by the mobile element potassium. This apparently quick mineralisation of phosphorus may enable the roots to re-absorb it during late autumn, possibly aided by mycorrhizas, before their activity declines in the winter, thus ensuring its re-cycling. The fact that a somewhat greater proportion of the phosphorus which returns both as litter (see table 2) and as leachate<sup>3</sup> does so during the spring and summer, will similarly aid retention of this element within the cycle.

At Meathop, lysimeter studies suggest that the amounts of phosphorus lost by soil drainage are so small as to be more than balanced by atmospheric income. Nevertheless, experiments carried out into the nutrition of oak seedlings at Bogle Crag suggested that this site is deficient in phosphorus as far as seedlings are concerned, and hence perhaps for the ecosystem as a whole.

#### *Ecosystems compared*

A comparison of Bogle Crag and Meathop can be made from the above-ground data presented in table 5. Although it can be seen that Bogle Crag had consistently lower figures for nutrient quantities than Meathop, reflecting the lower productivity both of woody material and foliage, the differences cannot solely be explained in this way. The *proportions* (shown as percentages in the table) of the total annual uptake which are retained within the tree increment are also consistently lower at Bogle Crag. If a further comparison is made with comparable data taken from Duvigneaud and Denaeyer-De Smet<sup>17</sup> for mixed oakwood at Virelles, Belgium, a site yet more productive than Meathop, the proportions withdrawn are greater still, with 31% of the nitrogen uptake, 22% potassium, 31% calcium, 28% magnesium and 35% of the phosphorus uptake being retained in the above-ground increment. These increased proportions are achieved however without an increased absolute uptake, except for calcium; magnesium uptake is very similar to Meathop, that for nitrogen, potassium and phosphorus somewhat less. A possible interpretation is that although absolute uptake of nutrients may, on the poorer sites, be similar to or even greater than that for the better areas, the proportions which the system can afford to remove from the cycle into increment is low. Conversely, correspondingly higher proportions (or even absolute amounts) are needed for cycling in order to keep the system functioning under adverse site conditions.

Ecosystems may also be compared on the basis of the distribution of the total nutrient capital between the various parts—total vegetation biomass, including roots, the undecomposed litter and the reserves in the soil. Data for Bogle Crag being incomplete, only Meathop and Virelles are compared here, in table 6. The proportions of the total 'available' capital (ie excluding the non-exchangeable fraction in the soil) present in the vegetation and litter are also shown as percentages. Whilst figures for nutrient distribution at the two sites are in general very comparable, differences

TABLE 6

Comparison of nutrient distribution in Meathop (Westmorland) and Virelles (Belgium from Duvigneaud and Denaeyer-De Smet<sup>17</sup>)  
(Kilograms/hectare)

	N		K		Ca		Mg		P	
	Meathop	Virelles	Meathop	Virelles	Meathop	Virelles	Meathop	Virelles	Meathop	Virelles
Annual retention in increment	24	30	13	16	30	74	6.1	5.6	1.7	2.2
Tree biomass	716	495	416 (56%)	296 (56%)	828 (43%)	1204 (8%)	145 (60%)	97 (37%)	44.1 (52%)	39
Ground flora biomass	22	38	16 (2.1%)	46 (8.6%)	8 (0.4%)	44 (0.3%)	3 (1.2%)	5.4 (2.0%)	2.1 (2.5%)	5.1
Undecomposed litter	180	44	49 (6.6%)	17 (3.2%)	237 (12.2%)	107 (0.7%)	24 (9.9%)	5.1 (1.9%)	7.6 (8.9%)	1.9
Soil 'available'*			249 (34%)	157 (30%)	840 (43%)	13600 (89%)	64 (26%)	151 (57%)	29.4 (35%)	
Soil 'non-available'	5550	4480	24100	26600	1440	119400	15600	6310	969	920
Total 'available' capital			743	532	1943	15029	242	264	84.8	

Note: Root data are included in the biomass and increment figures. Some of the Meathop data are provisional and subject to revision in Satchell<sup>1</sup>.

\* Extractable in ammonium acetate, pH 7, at Meathop (except P for which an isotopically exchangeable figure was determined). Virelles data given as exchangeable quantities.

occur reflecting, on the one hand, differences in available bases (potassium, calcium and magnesium) in the two soils and, on the other hand, the apparently greater rate of litter decomposition at Virelles. These differences apart, the broad picture provided by both these mixed oakwoods is similar to that found in other temperate deciduous woodland. Between about a third and two thirds (37–60%) of the total 'available' nutrient capital is locked up in the roots, stems and branches of the trees (except for calcium at Virelles). Smaller amounts are immobilised in litter, although these are still significant, especially if seen in relation to the requirements for the annual increment, which they generally exceed. These proportions may be contrasted, on the one hand, with the northern coniferous forests and, on the other, with tropical rain forests. In the northern forests, the proportions of the nutrient capital in the undecomposed litter can be at least as high as, or even considerably higher than, those in the biomass owing to a much slower rate of litter decomposition<sup>19</sup>. Conversely, in the tropical rain forest, most of the nutrient capital is in the biomass; there is virtually no litter accumulation because of its extremely rapid decomposition; and because of the high rainfall the major pathway for the return of nutrients to the forest floor is in fact by leaching<sup>20</sup>.

#### Effects of perturbations

The prospect of understanding or predicting the effects of 'perturbations', or disturbances, on an ecosystem is one of the objectives of whole-ecosystem studies. It is therefore appropriate to see whether the present information is at least sufficient to produce hypotheses, in two cases which appear relevant in this context.

##### 1. *Defoliation by Tortrix viridana*

Although the role of herbivores in the oakwood nutrient cycle appears to be small under normal circumstances, it is worthwhile considering their significance on those occasions when appreciable defoliation does occur. In his studies of *Tortrix viridana* defoliation at Roudsea Wood, which contains both slate and limestone woodland, Satchell<sup>21</sup> noted that severe defoliation was restricted to the areas of slate. This is probably also true for the southern Lake District generally, and may relate to the species poverty of these woodlands on acid soils. The virtually pure oak on many of these sites is almost certainly an artefact deriving from the former high value of oak which was favoured either by planting or otherwise<sup>22</sup>. These woods are therefore relics of a former commercial monoculture, prevented by grazing from becoming more diverse, and of which Bogle Crag is typical.

At this site, 1961 was a year of moderately severe defoliation by *Tortrix* in which 27% of the mean number of leaves or 25% of the mean leaf area in the sample plot were eaten by the larvae in May–June. A new flush of leaves was produced in early July, although sampling suggested that this replacement was about 10% less than the initial defoliation. Potential for photosynthesis was therefore



reduced not only during the period of larval activity, and in particular during the long days of midsummer which are likely to be of special importance<sup>23</sup>, but also to some extent for the remainder of the season.

TABLE 7  
Comparison of nutrients which would be removed in defoliation,  
with those retained in annual increment: Meathop  
(Kilograms/hectare)

	N	K	Ca	Mg	P
Annual increment requirement (including root-growth) . .	24	13	29	6	1.7
Leaf content at seasonal max.	97	47	47	10	6.4

Defoliation may however be even more severe, with many trees made completely leafless<sup>24</sup>. The reduction in oak increment following defoliation which has been demonstrated by a number of authors (eg Varley and Gradwell<sup>23</sup>) may not be solely due to the reduction in photosynthesis. Defoliation occurs when both the weight of leaves and their nutrient content are at or near the seasonal peak; the internal circulation of nutrients already referred to—especially important for nitrogen and phosphorus—is thereby entirely prevented. Replacement of this foliage in the new flush of leaf expansion, therefore represents a considerable drain on the trees' reserves of both organic materials and nutrients. The significance of this loss of reserves can be judged if the defoliation losses are compared with the requirements for nutrient retention in the trees' annual increment. Although absence of root data prevents such a comparison being made for Bogle Crag, the Meathop results in table 7 show that the loss of leaves (at the seasonal maximum) would remove the equivalent in nitrogen and phosphorus, and almost the equivalent for potassium, of the amounts required in four years total annual tree increment. It may be significant that Varley (quoted in Carlisle et al<sup>2</sup>) found that artificial defoliation in May of a small oak tree, produced virtually no stem increment for at least three years.

Defoliation by *Tortrix viridana* can occur for several years in succession once its numbers have built up sufficiently<sup>21</sup>. Even though materials remain within the system the repeated replacement of leaves during such outbreaks is nevertheless likely to make demands on the trees' nutrient reserves very much greater than can be supplied by re-cycling, with concomitant increment loss, unless mineralisation and uptake rates can both be increased several-fold.

Rafes<sup>25</sup> has pointed out, on the other hand, that some partially compensatory mechanisms may be associated with defoliation, including the possibility that the decomposition of litter might be speeded up both by the addition of easily mineralised nutrients in the frass, and by the extra insolation resulting from the reduced canopy.

## 2. *The effects of cropping*

Phosphorus supply and its circulation appear to be key factors in the oakwood ecosystems and, as far as Bogle Crag and other slate sites are concerned, where increment is very low, deficiency in phosphorus is possibly a main factor limiting growth. This very low productivity has in the past inhibited foresters from retaining oak on such sites. Although there may well be a variety of reasons for such slow growth, it is none the less of interest to see whether any light is thrown on the problem by examination of a somewhat speculative nutrient balance-sheet which it is possible to derive from existing data.

Natural losses of nutrients by drainage are small and tend to be more than balanced by income. These woods are not natural, however, and have been managed for centuries, with nutrient removal in the produce. Although such cropping would occur only at intervals—long or short depending on whether standards or coppice were removed—it may be assumed to be on average equivalent per year to the annual increment. It must be further assumed that nutrient retention in the increment of a coppice stand is similar to the figures available for high forest; and that the existing data for foliage adequately represent those for the foliage which would be present at the end of a coppice cycle (when the canopy would be at least as dense). The Bogle Crag data are given in table 8 and suggest that, if the stems only are harvested—the most likely situation today under high forest conditions—an annual cropping loss equal to the increment is more than balanced by atmospheric income. In former times, however, and especially under a coppice system,

TABLE 8  
Mean annual atmospheric income, and possible mean  
annual cropping losses of nutrients: Bogle Crag  
(Kilograms/hectare)

	N	K	Ca	Mg	P
(1) Atmospheric income*	(N-fixation)	5.8	8.5	14.5	0.40
(2) Retention in stem increment ..	1.2	1.0	1.0	0.10	0.10
(3) Retention in stem and branch increment	2.5	1.9	1.5	0.25	0.29
(4) Leaf content at seasonal maximum	105.4	24.2	26.3	6.6	6.6
(5) $1/14 \times (4)$ (Mean leaf removal in 14 year coppice cycle) .. ..	7.5	1.7	1.9	0.5	0.5
(6) Maximum possible removal in coppicing (3)+(5) .. ..	10.0	3.6	3.4	0.75	0.79

\* includes a notional figure for aerosols taken from Meathop data

the branch-wood was also utilised and the quantities of nutrients so removed are also shown in the table. Most of the Lake District woods were in fact coppiced, providing a variety of produce. Oak was the most valuable species; partly through the variety of uses to which all sizes of its wood could be put, including the manufacture of enormous quantities of charcoal required in the iron-smelting industry; and partly because of the high value of its bark, used in tannery. Because bark-removal and the splitting of the stems or branches necessary for many of the other uses were both much easier after the sap had risen in the spring, oak was the last species to be cut, some, if not all being left until May, June or even early July<sup>26</sup>. By this time, therefore, not only would the trees have been in leaf but, as was noted earlier, the nutrient content of the foliage at least, if not the tree as a whole was approaching its maximum. All parts of the felled trees were almost certainly removed from the site; there is evidence that even the foliage and twigs were burnt in special pits or cauldrons to provide potash which was used in the manufacture of the soft-soap or lye required for cleansing the fleeces or fulling the cloth in the extensive local wool industry<sup>26</sup>. Potash was also produced by burning bracken, which has a high potassium content. On the basis of a 14-year coppice cycle (records give a range of 12–16 years) an additional average annual loss would result from foliage removal, shown in line 5 of table 8. Although some of the high foliar nutrient content in spring may result from an internal redeployment of materials and not be due solely to uptake, it is apparent that delay in cutting until May-June would have led to a marked increase in nutrient loss, especially of phosphorus, which could have exceeded the income for this element. These losses may have been increased even more by burning bracken if it was present in the woodlands in worthwhile quantities. In the context of the above remarks it is noteworthy that most of Bogle Crag Wood is almost pure oak; that it was managed as coppice until about 1880; and that bracken is a dominant component of the ground flora. Dependent, therefore, on the rate at which nutrients in the soil are made available by weathering of the soil parent material, or by other release phenomena, the possibility exists that the relatively intensive cropping systems of the past have built up a phosphorus deficit within ecosystems like Bogle Crag. Even small losses in drainage might significantly influence the balance in such circumstances. On the other hand, the inherently more fertile soils of the limestone may have been able to withstand cropping losses which, because of higher productivity, would have been correspondingly even greater.

### Conclusion

In the moist climate of north-west England where shortage of water can rarely be an important factor, the productivity of an ecosystem will be largely dependent on nutrient availability, which in turn partly depends on nutrient cycling. However, the very limited

comparisons between oakwood ecosystems which have been made here suggest that the rate of nutrient cycling is not related in any simple manner with productivity. Data from more sites are necessary however, before this point can be clarified; indeed, only by studying a range of sites will it be possible to understand more fully the significance of nutrient cycling in ecosystem functioning.

At the same time it is clear that the functioning of an ecosystem is also dependent on factors which appear unimportant in nutrient cycling terms. For example, the limited significance of herbivores and other animals in the nutrient cycles of most forest systems<sup>27</sup> inadequately reflects their role in such ecosystems. They almost certainly play an important part in influencing woodland structure and dynamics by selective feeding (for example of seedlings and apical meristems), by seed dispersal, and no doubt in a variety of subtle ways, the importance of which is quite other than via nutrient cycling.

Nevertheless, a sufficiently useful model of the ecosystem can be derived from nutrient cycling studies to demonstrate their contribution to an overall understanding of how the system functions; to help in understanding the effects of management; and in generating hypotheses for a variety of problems.

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